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## Dependence of settlement rate on suitable substrate area

Received: 27 May 1997 / Accepted: 10 June 1997

**Abstract** Several recent field studies have found disproportionately high barnacle settlement rates (expressed on a per-area basis) in situations where the amount of suitable substrate is reduced, either due to occupation by other individuals or to physical processes. We call this phenomenon the intensification effect; it is not included in many models of benthic populations, which assume that the per-area settlement rate is a constant, or in field larval-collector studies, where number of larvae caught is assumed to be a function only of larval supply. In this paper we derive a simple Markov chain model that generates the intensification effect. It describes the fate of a settling larva, which may be washed out of the system or may attempt to settle in suitable or unsuitable substrate. If it lands on unsuitable substrate, it returns to the water column to try again. At low values of the washout rate, the per-area settlement rate decreases with increasing substrate area. At high values of the washout rate, per-area settlement rate is constant. We conducted a set of laboratory experiments in March through April 1995 with barnacle larvae (*Semibalanus balanoides* Linnaeus) to illustrate the predictions of the model. Substrate area was manipulated by varying the number of settling panels available, and the larval loss rate was adjusted by manipulating the residence time of larvae in the experimental units (1.5 h or 12 h). As predicted by the model, in the 12-h treatment settlement per area decreased nonlinearly as the amount of substrate increased, whereas in the 1.5-h treatment no differences were found. These results explain and predict the intensification effect, and suggest that variability in the proportion of suitable substrate may be an important factor in determining variability in settlement rate.

### Introduction

The larval phase of marine species critically influences such population phenomena as age-class strength (Hjort 1926), population fluctuations correlated with life history (Thorson 1950; Coe 1956), and uncorrelated densities of recruits and adults (Loosanoff 1964). Settlement and recruitment estimates have been used to compare larval input from the plankton, in spatial data or temporal series. Studies of fluctuations in settlement have focused on biological and physical factors influencing the settling larva. For example, Connell (1985) recognized three factors influencing invertebrate settlement rate: the number of propagules arriving, the site-specific hydrodynamic conditions, and behavioral factors. The resident assemblage of species can also influence settlement (e.g. Strathmann et al. 1981; Young 1988; Osman et al. 1989; Osman and Whitlatch 1995).

Larvae of sessile species in hard-surface communities require space to settle. Their impact on population dynamics will depend on how settlement is affected by availability of free space. Many studies of barnacle settlement have documented the influence of substrate characteristics on the choice of alternative substrates and settlement [presumably related to behavior of the cyprid stage; Pyefinch (1948); Connell (1961); LeTourneaux and Bourget (1988)]. We are not concerned here with these differences, but with the effect of the amount of suitable substrate, defined here as free space upon which larvae will settle.

Few studies have examined this effect; those that have, draw differing conclusions. Gaines and Roughgarden (1985), Navarrete and Castilla (1990), and Minchinton and Scheibling (1993) observed in the field that settlement was proportional to suitable substrate: the more substrate, the more total settlement. Other field studies suggest, however, that as suitable substrate becomes scarce, settlement per unit area intensifies. Bertness et al. (1992) found that the settlement per unit area of *Semibalanus balanoides* increased late in the season,

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Communicated by J.P. Grassle, New Brunswick

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apparently as a result of favorable sites being filled by settlers early in the season. Pineda (1994b) found that settlement per unit area of the barnacles, *Chthamalus* spp., was consistently higher at the edges of a rocky shore, where suitable settlement area was scarce, than at the middle of the rocky beach, where suitable substrate was abundant, suggesting higher settlement per unit area in areas with less suitable substrate. At another rocky shore, some areas of the intertidal zone were seasonally inundated by sand, an unsuitable substrate for barnacle settlement. Areas with more sand – less suitable substrate – received predictably higher settlement per unit area than areas not invaded by sand. This ranking disappeared when the sand was not present, suggesting that the ranking was maintained by differences in the amount of suitable substrate. These observations resulted in the development of the “decreased-substrate settlement-intensification hypothesis” (Pineda 1994b) according to which the per-area settlement rate is a decreasing function of available substrate. Hunt and Scheibling (1996) observed enhanced mussel settlement in settlement collectors relative to ice-scoured emergent rocks, and suggested that settlement intensification could be related to unsuitability of ice-scoured surfaces. Osman and Whitlatch (1995) compared settlement panels with high, low, and no adult cover. They observed that settlement density of several sessile taxa was often higher in treatments with the highest density of adults, and suggested that settlement could be intensified in these panels due to larvae rejecting adults as substrate, and then swimming a short distance to settle on open substrates; this would result in a settlement intensification effect. They created a model incorporating larval discrimination, probability of settlement on adults, on free substratum, and probability of larvae being removed from the substratum. Their model predicts that the pattern of intensification is determined “by the mobility of the larvae that fail to attach”.

Settlement rate can be measured in various ways (Table 1), and for the present study we are careful to specify which rates we are talking about. These are made clear in the population models of Roughgarden et al. (1985) and Roughgarden and Iwasa (1986), which identify an important set of hypotheses about the relationship between settlement and suitable substrate (free space, in their notation). Let  $B(t)$ ,  $L(t)$ , and  $F(t)$  be the numbers of adults, larvae, and the suitable substrate within the region under consideration. Then

$$\frac{dB(t)}{dt} = c F(t)L(t) - \mu B(t) \quad (1)$$

**Table 1** Some definitions of settlement rate ( $N$  number of individuals;  $t$  time)

Designation	Units	Description
Net settlement rate	$N t^{-1}$	Total settlement per unit time
Per-capita settlement rate	$t^{-1}$	Settlement per-larva per unit time
Per-capita, per-area settlement rate	$\text{area}^{-1} t^{-1}$	Settlement per-larva per unit area per unit time
Per-area settlement rate	$N \text{area}^{-1} t^{-1}$	Total settlement per unit area per unit time

$$\frac{dL(t)}{dt} = m B(t) - \lambda L(t) - cF(t)L(t) \quad (2)$$

$$F(t) = A - aB(t) \quad (3)$$

where  $\mu$  and  $\lambda$  are mortality rates,  $m$  is the reproductive rate,  $A$  is the total space,  $a$  is the mean size of an adult, and  $c$  is a constant of proportionality (in units  $\text{area}^{-1} t^{-1}$ ). The first term in Eq. 1, which is also the last term in Eq. 2, gives the *net settlement rate*,  $cF(t)L(t)$ , in units of  $N t^{-1}$ , where  $N$  is number of individuals. Settlement rate can be expressed in other units by dividing  $cF(t)L(t)$  by the appropriate term. The *per-capita settlement rate*, (in units of  $t^{-1}$ ) is obtained by dividing by  $L(t)$ . The result is  $cF(t)$ ; i.e. in this model per-capita settlement rate is directly proportional to suitable substrate. The *per-capita, per-area settlement rate* (in units  $\text{area}^{-1} t^{-1}$ ) is given by the constant  $c$ . Finally, the *per-area settlement rate* (in units  $N \text{area}^{-1} t^{-1}$ ) is  $cL(t)$ , and is hence assumed to be independent of suitable substrate, but directly proportional to larval abundance.

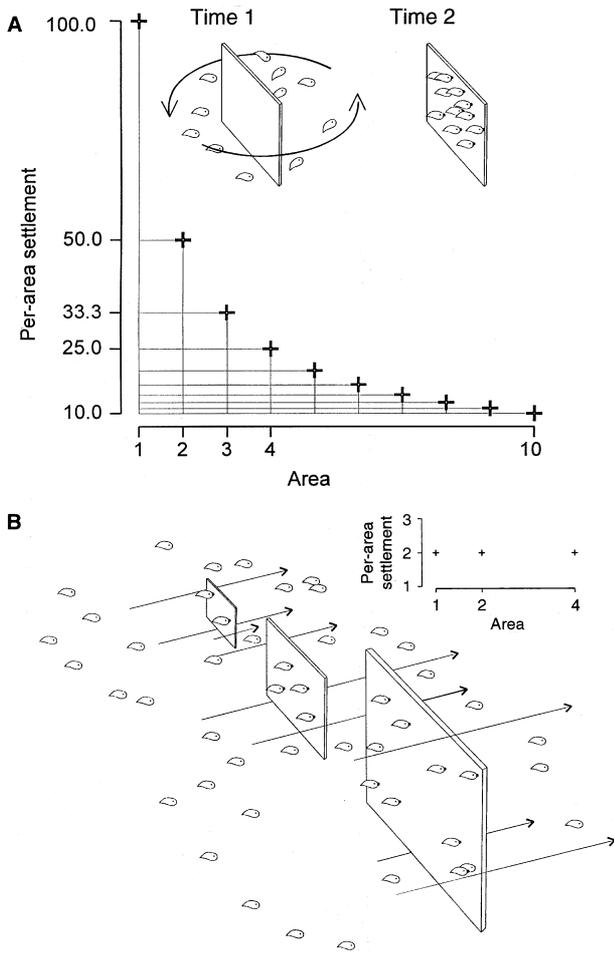
This model is a useful first approximation to the settlement process, and agrees with some field data (Gaines and Roughgarden 1985; Minchinton and Scheibling 1993), but as pointed out above, there is evidence that per-area settlement is not independent of suitable substrate.

In the present study, we develop a simple settlement model that includes aspects of larval behavior (larvae may test the substrate repeatedly to locate a suitable area) and of environment (a washout rate determines how many attempts a larva may make before being lost from the system) that are not included in the simple formulation of Eqs. 1 to 3. Our model predicts the intensification of settlement with decreased substrate area reported by Bertness et al. (1992), Pineda (1994b), Osman and Whitlatch (1995), and Hunt and Scheibling (1996). We also present results of a laboratory settling experiment that illustrate this phenomenon. The objective of the experiment is to mimic only the basics of the model mechanics.

## Materials, methods and results

### Geometric decrease in settlement with increasing area

Consider a volume of water with a number of competent larvae  $L$  settling in an area of suitable substrate  $F$ . Settled larvae are  $N$ . If the residence time of water around the substrate is long, then all the larvae will eventually encounter the substrate and settle. Then  $L = N$ , and the per-area settlement rate is  $S = L/F$ . Doubling  $F$



**Fig. 1** Schematic representation of the decreased-substrate settlement-intensification hypothesis. **A** The graph shows that a constant number of larvae (100) settle in the suitable substrate. As suitable substrate increases, per-area settlement decreases geometrically. The drawing shows that all the larvae around the plate in time 1 settled in time 2. (Back of plate is unsuitable.) **B** The graph shows that per-area settlement is similar in all areas. The drawing shows that settlement per unit area is proportional to the concentration of larvae in the water. Only larvae encountering the substrate settle

yields,  $S = 1/2(N/F)$ , tripling it,  $S = 1/3(N/F)$ , and so on. Increasing settlement area linearly yields a geometric decrease in the settlement per unit area (Fig. 1A). Consider now larvae with less chance of encountering the substrate. For example, water flowing perpendicular to a settlement substrate (Fig. 1B), where only those larvae encountering the substrate settle, and residence time of the water around the substrate is very low. Now the probability of encountering the substrate is proportional to the area of the substrate, so that  $N \propto LF$ . In this case,  $S \propto LF/F$ , and doubling  $F$  would yield  $S \propto 2/2(LF/F)$ , tripling it  $S \propto 3/3(LF/F)$ , and so on. Settlement per unit area is now dependent only on the concentration of the larvae in the water, with no intensification effect due to differences in  $F$ . This agrees with the per-area settlement rate assumed in Eqs. 1 to 3.

**The model**

In this section we describe a simple Markov chain model for larval settlement that incorporates the following factors: (1) a specifiable amount of suitable substrate, expressed as a proportion  $p$  of the total space; (2) a specifiable rate of loss (a “washout” rate) of larvae

from the area; (3) the possibility for a larva that encounters unsuitable space to return to the water column and attempt to settle again, although in doing so it again incurs the risk of washout. Note that, although we use the term “washout” for convenience, because we suspect that in most cases hydrodynamic factors will strongly influence this rate, the model does not make any assumptions about the mechanism of loss. In particular, it does not require the assumption that larvae act as passive particles. It does, however, assume that the larvae settle at random, so that the probability of encountering suitable substrate is equal to the fraction of total space that is suitable.

The model describes the fate of a larva in the water column over a short time interval (Fig. 2). It may be washed out of the system with probability  $w$ . If it is not washed out (which occurs with probability  $1-w$ ), it will settle, landing on suitable substrate with probability  $p$  and on unsuitable substrate with probability  $(1-p)$ . If it settles on suitable substrate, it stays there. If it attempts to settle on unsuitable substrate, it returns to the water column where it repeats the process. The resulting transition matrix is

$$A = \begin{bmatrix} 1 & 0 & 0 & p(1-w) \\ 0 & 1 & 0 & w \\ 0 & 0 & 0 & (1-p)(1-w) \\ 0 & 0 & 1 & 0 \end{bmatrix} = \begin{bmatrix} \mathbf{I} & \mathbf{R} \\ \mathbf{0} & \mathbf{T} \end{bmatrix} \quad (4)$$

The model contains two absorbing states (settled on suitable substrate and lost) and two transient states (in the water and attempting to settle on unsuitable substrate). The submatrix  $\mathbf{R}$  describes transitions from the transient states to the absorbing states; the submatrix  $\mathbf{T}$  describes the transitions among the transient states.

The model describes the fate of an individual larva. In a steady state, in which larval arrival balances larval loss, the probabilities of an individual larva are the same as the proportions of a cohort of larvae. Thus our results apply directly to open systems.

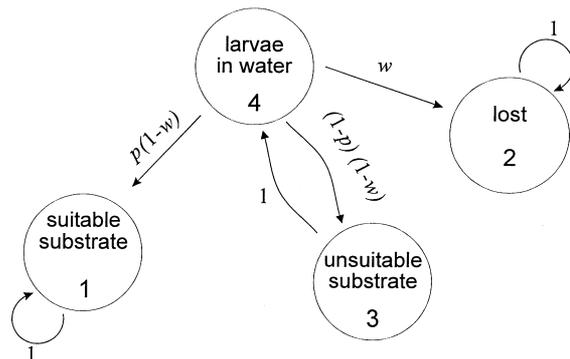
Standard results in Markov chain theory imply that a larva is destined, with probability 1, to end up in one of the two absorbing states. The probabilities of absorption in each of these two states is given (e.g. Iosifescu 1980, Theorem 3.3) by the entries of a matrix

$$F = \mathbf{R}(\mathbf{I} - \mathbf{T})^{-1} \quad (5)$$

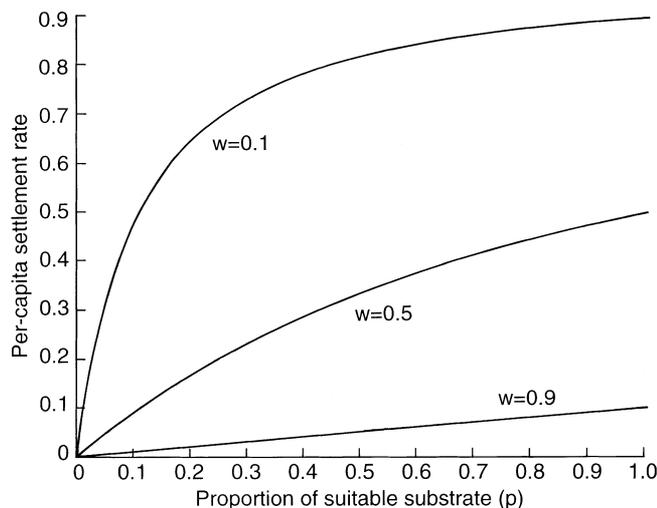
where  $f_{ij}$  is the probability of absorption in absorbing state  $i$  given that the larva starts in transient state  $j$ . For our model, this matrix is given by

$$F = \begin{bmatrix} \frac{p(1-w)}{w+p(1-w)} & \frac{p(1-w)}{w+p(1-w)} \\ \frac{w}{w+p(1-w)} & \frac{w}{w+p(1-w)} \end{bmatrix} \quad (6)$$

The probability that a larva in the water eventually settles successfully (i.e. the per-capita settlement rate) is given by  $f_{11}$ . The per-capita, per-area settlement rate is thus  $f_{11}/p$ :



**Fig. 2** Transition structure of the model.  $p$  is the probability of a settling area encountering suitable substrate and  $w$  is the probability of a larva being lost to the system



**Fig. 3** Model results for per-capita settlement rate as function of proportion of suitable substrate  $p$  at different  $w$

$$\text{per-capita settlement} = \frac{p(1-w)}{w+p(1-w)} \quad (7)$$

$$\text{per-capita, per-area settlement} = \frac{1-w}{w+p(1-w)} \quad (8)$$

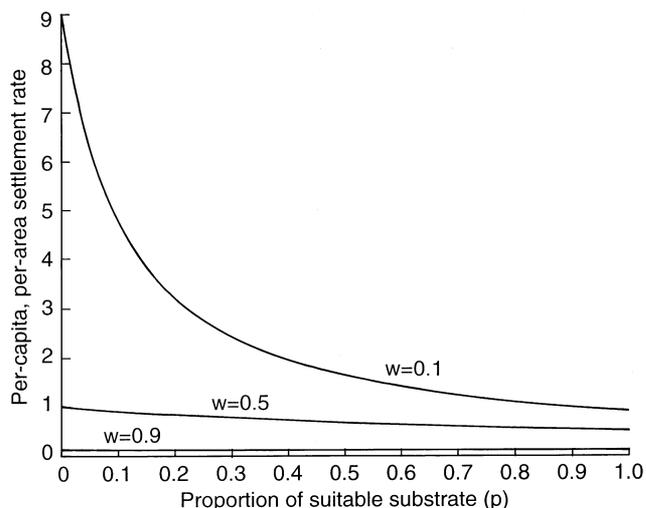
The resulting rates as functions of the proportion of suitable substrate  $p$  and the washout rate  $w$  are shown (Figs. 3, 4). In situations with high washout rates, where a larva rarely has more than a single chance to settle, the per-capita settlement rate increases linearly with  $p$  and the per-capita, per-area settlement rate is constant. In situations with low washout rates, however, the per-capita settlement rate is a decelerating function of  $p$ , and the per-capita, per-area settlement rate declines with increasing  $p$ .

The combination of low washout rate and the possibility of repeated settlement attempts together generate an intensification of settlement as suitable substrate becomes rare, as described in the "Introduction".

#### Experiments on barnacle settlement

In order to examine these two mechanisms in a simplified laboratory setting, we carried out a series of experiments on barnacle cyprids (*Semibalanus balanoides* Linnaeus) in plastic trays. Suitable substrate was provided by grooved ceramic tiles, unsuitable substrate by the smooth surface of the plastic trays, on which few larvae settled. Since in the model the washout rate is inversely proportional to the mean residence time of a larva, we manipulated the length of time (1.5 and 12 h) the larvae were exposed to the settling plates. This corresponds to an eight-fold increase in  $w$ .

The experiments were conducted from 25 March to 18 April 1995 using barnacle cyprids. A sample of zooplankton was collected from Eel Pond (Woods Hole, Massachusetts) with a mesh net. Large debris and large zooplankton were removed manually from the net. Field samples were heavily dominated by barnacle cyprids. The mesh was gently washed with filtered seawater and the larvae transferred to a clean glass jar. The water containing the concentrated larvae was then split with a Folsom plankton splitter into four portions, and each portion was added to an experimental tray (see below). Because of their tendency to settle rapidly, we attempted to minimize the exposure of larvae to hard surfaces during handling. Although we did not identify the cyprids, Fish (1925) found that in March through April the only cyprids in the Woods Hole region were *Semibalanus balanoides*, with other barnacle species breeding in other seasons. We assumed that all cyprids



**Fig. 4** Model results for per-capita, per-area settlement rate as function of proportion of suitable substrate  $p$  at different  $w$

were *S. balanoides*. Experiments were done in still water in  $27 \times 38$  cm plastic trays. Grooved ceramic tiles ( $11.2 \times 11.2$  cm) were used as settlement substrate. Each tile contained 2  $A$  unit areas. To obtain 1 unit areas ( $11.2 \times 5.6$  cm) half a single tile was wrapped with new aluminum foil. Tiles were rubbed with a mixture of ground *S. balanoides* barnacles and seawater (reviewed by Crisp 1976), exposed to this mixture for at least 1 h, and then gently washed just prior to the experiments. Tiles rested horizontally (finished sides down, grooved sides up) on glass vials  $\approx 4.5$  cm above the bottom and  $\approx 1.5$  cm below the surface of the water. Tiles were placed contiguously at the center of the trays. For each run (see below), four plastic trays were haphazardly arranged inside a larger seawater table. Seawater at ambient temperature ( $\approx 6$  to  $9^\circ\text{C}$ ) flowed continuously in the large water table, immersing  $< 1$  cm of the experimental trays. Experiments were done in the dark by covering the seawater table with black plastic. Trays were thoroughly washed with freshwater and exposed to the sunlight between experiments.

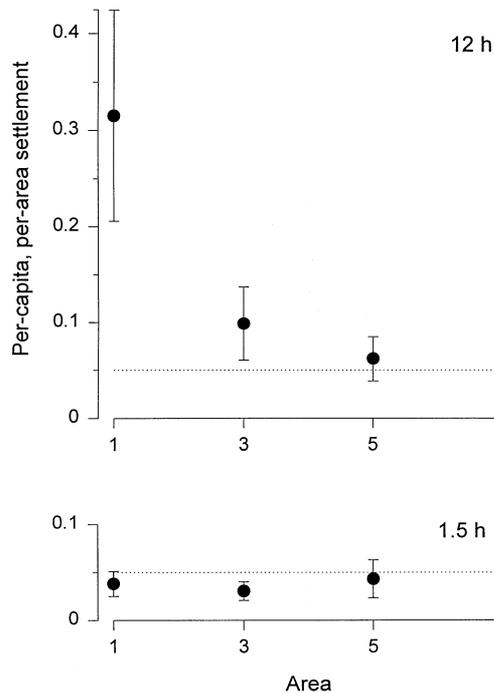
We manipulated  $p$  by varying the number of settling panels (1, 3, 5 and 7 areas, corresponding to 62.7, 188.2, 313.6, and 439  $\text{cm}^2$ ) and  $w$  by varying the amount of time available for settling (1.5 and 12 h). Areas and times were chosen arbitrarily. There were eight treatments ( $2 \times 4$  areas) which were replicated five times. Four treatments (all areas for either 1.5- or 12-h treatments) were run at a time. The sequence of the treatments followed a randomized block design in time where each four treatments constituted a block.

At the end of the experiments, tiles were removed from the plastic trays and attached larvae were counted. The remaining live larvae in the experimental trays were filtered and counted. Field samples contained dead larvae that were not counted prior to the experiment to minimize manipulation. These were quantified only after the end of the experiment. We assumed that dead larvae originated in the field, with no mortality occurring during the experiments. The total number of larvae per experimental tray (alive + settled) ranged from 21 to 246 in the 1.5-h experiments, and 33 to 240 in the 12-h experiments.

We calculated the per-capita, per-area settlement rate as:

$$\left( \frac{\text{attached larvae on plates}}{\text{attached larvae on plates} + \text{filtered live larvae}} \right) \times \frac{1}{\text{number of areas}}$$

One 1.5-h run was repeated because there were very few larvae overall, both settled and in the tank.



**Fig. 5** *Semibalanus balanoides*. Area versus settlement per unit area results for the settlement experiment. One unit area =  $11.2 \times 5.6$  cm. Settlement was calculated as: [(attached larvae in plates)/(attached larvae in plates + filtered live larvae)]  $\times$  1/(number of areas)

#### Barnacle settlement results

Most cyprids attached to the treated tiles, with few settling on other surfaces (wall of plastic container, aluminum foil, etc.). Cyprids settling on substrata other than the treated tiles were not included in the analysis.

In the 12-h experiment there was a sharp decrease in the per-capita, per-area settlement rate with increasing area, but no differences were apparent in the 1.5-h experiment (Fig. 5). There was high inter-run variability in the proportion of live larvae that settled. Highest variability was found in the treatment for 12 h with only 1 unit of area, where proportions ranged from 0.79 to 0.13. Plots for individual runs showed that in four out of five cases individual functional relationships were similar to the averaged results (Fig. 5).

A two-way analysis of variance on square-root arcsine transformed data (Sokal and Rohlf 1979) showed evidence of significant differences in both area and time of experiment (Table 2; all significance tests at a  $\alpha = 0.05$ ). The area-time interaction was also significant, indicating that the area versus settlement functional relationships were different for the two times.

## Discussion

Our study was designed to illustrate the intensification phenomenon, an overlooked aspect of larval settlement.

In particular, our experiment was conducted in simplified laboratory conditions, and its objective was to mimic only the basic aspects of our model. We expect further complications as the washout rate, or the proportion of suitable substrate, are parametrized in field conditions.

Our experimental results agree well with the functional relationships predicted by the model. For the 12-h experiment there was a geometric decrease in per-area settlement with increasing suitable substrate size, but no differences were found for the 1.5-h experiment.

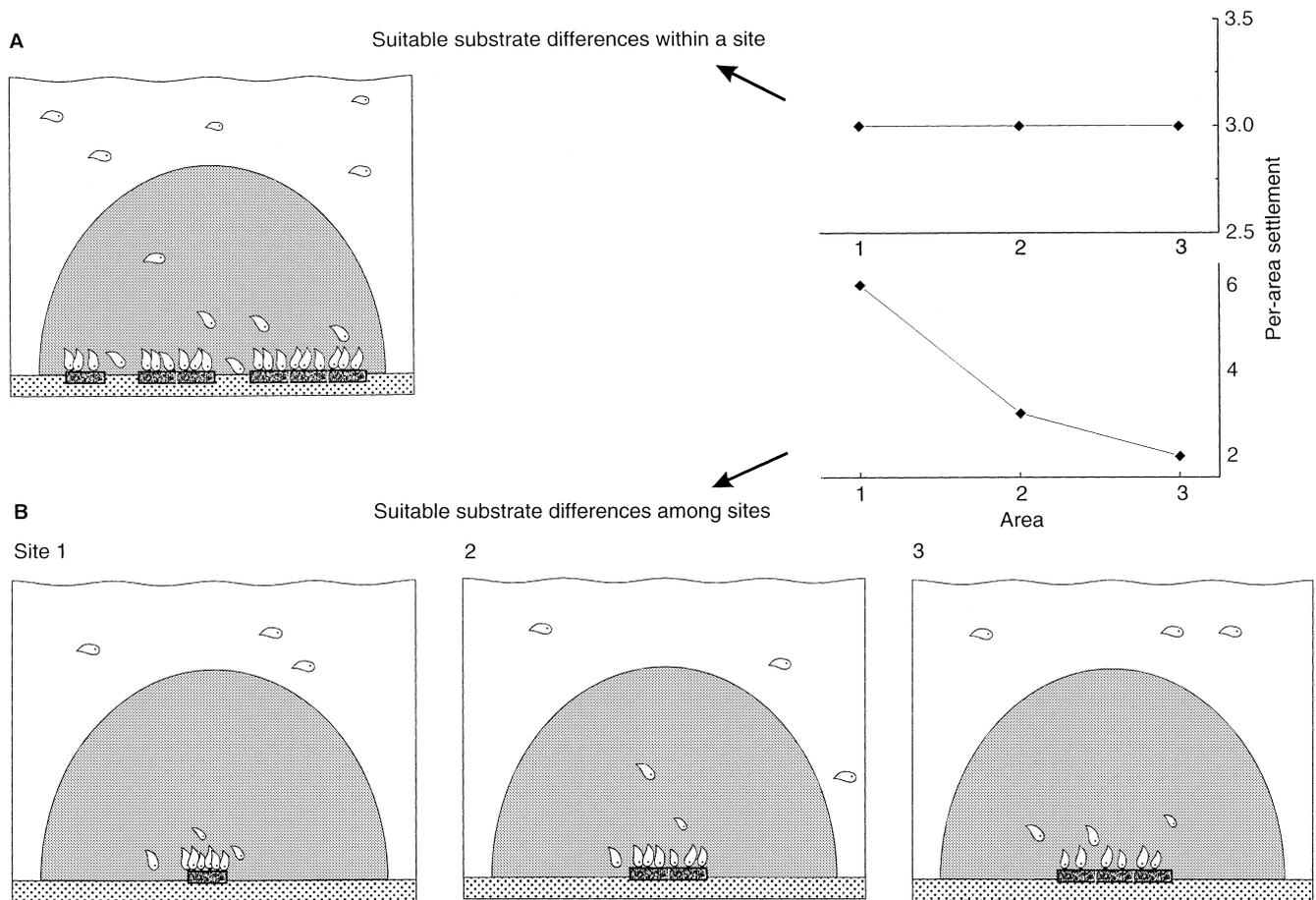
A potential behavioral factor influencing our experimental results is gregarious settlement. Settlement substrates with less area could have potentially concentrated more larvae at the beginning of the settlement process, due to the small area intensification effect. For larvae with gregarious behavior, the first larvae to settle would produce a positive feedback effect, attracting even more larvae. Gregarious settlement would add to the reduced substrate effects to produce even higher intensification effects. In this process the first-order phenomenon is the effect of small area, because with no small-area effect, there would be no gregarious intensification effect. *Semibalanus balanoides* is a gregarious settler (e.g. Barnett and Crisp 1979), and this effect could have influenced our experimental results in that it could have enhanced the geometric decrease in settlement density with increasing area. Our results do not allow us to discern whether there was a gregarious enhancement effect.

Osman and Whitlatch (1995) observed aggregation of settling larvae on open substratum near established adult ascideans, and created a model conceptually similar to ours to account for this phenomenon. While our model deals more generally with the question of substrate availability – only adult cover was considered by Osman and Whitlatch – both models make the same prediction, that as suitable substrate and the washout rate decrease, settlement density intensifies.

Studies on barnacle settlement rate on  $> 100$  m scales have generally found that a large portion of the temporal and spatial variability can be accounted for by physical transport processes (Shanks 1983; Farrell et al. 1991; Pineda 1991, 1994a; Gaines and Bertness 1992; Bertness et al. 1996). On smaller scales, behavior and micro-hydrodynamic processes may help to explain the observed patterns (e.g. Wethey 1983; Raimondi 1990). In field studies, artificial larval collectors or settlement plates are often used to measure settlement rate per unit area, and then rates at different heights within a site or sites along the shore or across the shore are compared.

**Table 2** *Semibalanus balanoides*. Two-way analysis of variance for the settlement experiment

Source	Sum of squares	df	Mean square	F-ratio	P
Time	723.20	1	723.20	10.57	0.003
Area	893.04	3	297.68	4.35	0.011
Time $\times$ Area	707.22	3	235.74	3.44	0.028
Error	2190.14	32	68.44		



**Fig. 6** Schematic representation of the scale dependence of the intensification phenomenon. Only the population of larvae within the gray areas can settle on the suitable substrate encompassed by the gray areas. **A** All suitable substrates occur under a common gray area; there is no intensification effect. **B** Different suitable substrates are under different gray areas. Assuming a similar number of larvae within each gray area, there is an intensification effect. This may also represent a single site at times 1, 2 and 3. Time variability in suitable substrate within a single site would produce time variability of the intensification effect

Consistent differences are interpreted as being due to rates of arrival of larvae, or behavior. Bertness et al. (1992), Pineda (1994b), Osman and Whitlatch (1995), Hunt and Scheibling (1996), and the present study show that consistent differences among field sites, or consistent differences over time in a single site, could be due to differences in availability of suitable substrate. Since the amount of suitable substrate in general varies on longer time scales (weeks to years) than the rate of input of the larvae (hours to days), this would tend to produce consistent differences in settlement in space or time.

At the community level in sessile invertebrates, it is known that patch size available for colonization influences recruitment as well as the final composition of the adult assemblage (Jackson 1977; Kay and Keough 1981; Keough 1984). Our results further strengthen the idea that settlement and recruitment may be dependent on

patch size, and add a possible mechanistic explanation as to why smaller areas of substrates receive higher recruitment rates (e.g. Jackson 1977).

The models of Roughgarden et al. (1985) and Roughgarden and Iwasa (1986) assume that the per-capita settlement rate is proportional to suitable substrate. In testing this assumption, Gaines and Roughgarden (1985) found that the relative number of cyprids settling in a portion of a small quadrat was directly proportional to the area of that portion. Minchinton and Scheibling (1993) found similar results, and Chabot and Bourget (1988) found that settlement was correlated with the amount of suitable substrate, but only when adult barnacle cover was  $> \text{ca. } 30\%$ . In the latter two studies it was suggested that behavioral factors could modify this simple relationship. Our results suggest that in cases where larvae can repeatedly sample the suitable and unsuitable substrate within the area results may be different to what these authors have found.

The discrepancy between the study of Gaines and Roughgarden (1985) and our results is probably due to the scale dependency of the intensification phenomenon (Pineda 1994b). Their results could be expected for very small-scale systems, such as the small subsectors ( $2.9$  or  $5.8 \text{ cm}^2$ ) within the  $34.6 \text{ cm}^2$  quadrats used in their study, or when there is no change over time in the

amount of suitable substrate within a site. When comparing different amounts of substrate within a small-scale system, total settlement may be directly proportional to suitable substrate because all suitable substrate is viewed as the same by the population of larvae. At larger spatial scales, settlement substrates would be separated far enough such that suitable substrate would be viewed as different by larval populations (Fig. 6). Because the amount of suitable substrate changes with time, intensification can also vary in time within a single site. Bertness et. al (1992) observed intensification as suitable substrate was occupied by early settlers, and Pineda (1994b) observed intensification as suitable barnacle substrate decreased in time due to sand inundation of the rocky intertidal zone.

We have shown that the decreased-substrate settlement-intensification effect depends on  $w$ , the probability of larvae being washed out of the system. In our experiment we varied  $w$  by varying the length of the experiment. The residence time of the water in the 12-h experiments is probably high when compared to field conditions. Comparing parameters in our simplified experiment with field conditions may be misleading. In the field, other processes will influence  $w$ , including residence times of the water, basin configuration, diffusion, and advection. In interspecific comparisons, larval size may also have an effect; for small larvae, higher diffusion rates would increase the probability of encountering the substrate, while higher advection rates would remove larvae from the system. If the diffusion rates are very high, however, the increased probability of finding the substrate might be countered by an increased probability of being washed out of the system. There is not an obvious answer for the relative roles of these variables, and their relative contribution would only become apparent with further work.

In the intertidal zone, the washout rate may be related to height with respect to sea level. Because the water in the lower intertidal zone has higher residence times per tidal cycle than the water at the higher intertidal, larvae would have a higher probability of encountering the substrate lower in the intertidal than in the higher intertidal. [Breaks in submersion times in the intertidal height gradient, with matching expected breaks in intensification effects, would correspond to Doty's (1946) critical tide levels.]

The intensification effect describes what happens over a range of  $p$ -values, the proportion of suitable substrate. If the suitable substrate area is large relative to the number of larvae, then one would not expect the intensification effect. What constitutes suitable habitat varies from species to species. Some species are more discriminating settlers than others. For example, *Chthamalus fissus* larvae are more indiscriminate than *Pollicipes polymerus* (Pineda 1994b), and *P. polymerus* adults appear to prefer high current-wave micro-environments (Barnes and Reese 1960). For highly discriminating settlers, suitable substrate is more restricted, i.e.  $p$  is very low. The intensification effect for such species,

assuming similar numbers of larvae, would then be higher than for less discriminating species.

In summary, our results explain and predict variability in the intensification phenomenon. They also caution about interpreting spatial and temporal variability in settlement rates solely in terms of differences in the rate of arrival of the larvae or behavior. Consistent differences in settlement rate might well be due to differences in the availability of suitable substrate. We also suggest it might be important to include this effect when modeling space-limited open populations.

**Acknowledgements** This research was supported by a W.H.O.I. postdoctoral fellowship, ONR grant N00014-92-J-1527 and NSF OCE9529626. This is Woods Hole Oceanographic Institution Contribution Number 9369. We thank A. Parés-Sierra for discussing some issues in this paper, R. Osman for pointing out important pertinent literature, and reviewers for careful readings of an earlier version.

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